CONSTANCY OF INCUBATION FOR THE SCARLET TANAGER

KENNETH W. PRESCOTT

THE recent and interesting paper by Alexander F. Skutch (1962) stimulated me to reexamine the incubation data which I had gathered on female Scarlet Tanagers (*Piranga olivacea*) in southern Michigan during 1947, 1948, and 1949. Utilizing his formula $T = \frac{100S}{S+R}$ to determine the percentage of constancy, I reworked the data for my ten females, arranging them in accordance with Skutch in Table 1. The average constancy, 77%, seems to fit nicely within the range of constancies given in his Table 2. Moreover, it falls within the range of constancy, 60–80%. mentioned by him as being "normal" for birds incubating alone and given food occasionally on the nest.

In reorganizing my data, it became apparent that additional columns of information might be helpful in interpreting the constancy of incubating females. For example, wherever possible, observations for individual females should be separated to show their patterns by the day of incubation, time of day, and average temperature. Table 2 shows these data for my ten females. Time of day is arbitrarily divided into three approximately equal divisions as: morning = dawn–09:00, midday = 09:00–16:00, and evening = 16:00–dusk. Where observation spanned somewhat equally two periods. they are so indicated. Temperatures recorded at ground level and in the shade each hour were averaged for the period. Arranged in this way, these factors may be examined for possible correlation with computed constancies. All observations were made from a blind and through a 20 power spotting scope supplemented with 7×50 binoculars. All times were computed to the nearest ½ minute with a sweep-second hand watch.

Influence of male on mate's constancy.—Skutch (op. cit.) suggests several ways in which the nonincubating male may influence the female. As is generally known. only the female Scarlet Tanager incubates. While she is occasionally fed on the nest by her mate, there appears to be considerable variation with some males feeding the incubating females often, and others rarely or not at all. It is quite possible that feeding of the incubating female on the nest by the male Scarlet Tanager does increase session length, although not significantly so. While males #1 and #10 fed their mates on the nest, I did not notice this for the other males. The average of female #1's constancies is 78.5% and that of female #10 is 82.1%. These are slightly, but probably not significantly higher than the averages for the other females:

TABLE 1

SUMMARY DATA FOR INCUBATION PATTERNS OF TEN FEMALE SCARLET TANAGERS AT TEN NESTS

Hours watched	No.*	Sessions in minutes		Recesses in minutes		Constancy %
		Range	Average	Range	Average	
114.5	267	0.5–71.5	19.5	0.5–41	5.8	77

* Number of sessions; number of recesses = 269.

FEMALE NO.	% CONSTANCY
# 3	74.5
# 5	59.3
# 6	75
#13	75
#15	80
#16	81
#17	85
#18	64.5

Males frequently feed the female within seconds after she leaves the nest. It would appear that these feedings are a contributing factor to shortening the recess length. This was particularly noticeable for females #10 and #17 whose patterns of remarkably short recesses seem the direct result of ready (almost instantaneous) feeding by the male. This is not the entire explanation for short recesses because females often darted from the nest to take insect food from leaves or branches which, apparently, they had sighted while still on the nest. Skutch mentions (op. cit.) that for the Orange-billed Nightingale-Thrush (*Catharus aurantiirostris*) and the Streaked Saltator (*Saltator albicollis*) the females' sessions were longer when the mates were not in sight, with the females' shorter periods apparently the result of the male appearing and/or calling. The male tanager is almost always close at hand in the territory and would usually be within her sight. I have many observations of the incubating female looking in his direction, at times changing position on the nest to face him, and occasionally leaving abruptly as he calls nearby. Sometimes (above) he feeds her but more often they forage together within the territory.

Temperament—Both Skutch (op. cit.) and Kendeigh (1952:40, 44, 89) suggest that individual differences of the females studied must be explained, at least in part, by innate individual characteristics. I was impressed by the quite individualistic behavior of the female tanagers, not only on the nest, but their manner of arriving and leaving, their response to the male, and other environmental circumstances. It seems that the constancies, length of

Table 2

Incubation Patterns of Ten Female Scarlet Tanagers at Ten Nests

Female	Day of incubation	Hours, minutes watched	No. of		Sessions in minutes		Recesses in minutes		Constancy %	Time of day			Average temperature F
			Sess.	Rec.	Range	Average	Range	Average		Morn	Mid	Eve	
1	1	3:07	7	6	9–29	19.28	2–20	8.66	69		x		
"	2	5:54	15	15	4–22	14.50	1–10	4.90	75		x		
"	5	3:21	14	14	5–15.5	10.53	0.5–9	3.35	76		x		
"	6	3:29+	8	7	6.5–36	18.68	0.5–5	2.93	86	x			
"	7	2:15+	6	6	1.5–36	17.83	1–9	4.67	79			x	
"	8	3:13.5+	9	9	2–56	18.83	0.5–7.5	3.17	86	x			
3	12	1:56	5	5	4–26	16.80	3–12	6.40	72			x	
"	13	4:46	10	10	3.5–39	22.00	0.5–14	6.70	77		x		
5	7	3:26	9	9	0.5–45	15.61	0.5–18	8.39	65	x			
"	9	2:30	6	5	2–23	13.16	7–34	14.20	48	x			
"	11	1:48	3	3	0.5–64	24.50	3.5–25	11.50	68			x	
"	12	1:08	2	2	3–30	19.00	1–29	15.00	56	x			
6	2	1:31	5	5	3–23	13.60	1–7	4.60	75	x			
10	1	5:36	12	12	5–55.5	23.00	1.5–10	5.00	82		x		76.2
"	2	2:25	6	6	5–36.5	21.58	0.5–8.5	2.58	89			x	66.2
"	3	4:15+	9	10	5–52	22.50	0.5–4.5	2.45	90	x			61.6
"	4	5:44.5	15	15	2–52	19.40	0.5–13	3.63	84		x		67.0
"	5	2:08.5	5	6	9.5–27.5	22.00	0.5–5.5	3.83	85		x		67.7
"	6	7:26	20	20	3–26	13.05	0.5–30	9.25	58		x	x	79.6
"	7	5:26+	8	8	1.5–71.5	39.67	0.5–20	6.17	87	x			68.3
13	1	3:04+	5	5	3.5–49	28.10	4.5–14.5	8.30	77	x			66.8
"	2	2:59.5+	4	5	25–36.5	30.63	5–28.5	11.40	73	x			42.8
15	1	1:44.5	5	5	11.5–22	16.80	3–6	4.10	80	x	x		58.4
16	1	1:49	3	3	29–33	30.33	5–7	6.00	81			x	79.3
17	8	3:22.5	6	6	3.5–55.5	29.50	3.5–5	4.25	87		x		74.5
"	9	3:01	6	7	6.5–39.5	25.83	1–5	2.29	92		x		56.0
"	10	3:25.5	10	10	7–35	17.95	0.5–6	2.60	87		x		61.5
"	11	3:14	7	7	9.5–42.5	24.43	1–5	3.29	88		x		64.9
"	12	3:37	10	9	4–33.5	18.65	1–8	3.39	85		x		71.5
"	13	5:84	14	15	1.5–35	18.71	0.5–21.5	7.77	71		x	x	80.3
18	1	2:07	6	6	7–18	13.75	5–10	7.42	65		x		78.3
"	3	2:50+	5	5	16–34	23.71	7–13.5	10.30	70			x	64.8
"	4	3:13+	7	8	11–32	20.21	1.5–11	6.44	76			x	67.0
"	5	2:07+	5	5	8–20	12.00	6–41	13.40	47			x	76.7

recesses, sessions, etc. for the females given in Table 2 do reflect to an unkown degree, individual variations.

Stage of incubation.—Skutch (op. cit.) raises several interesting questions concerning the day-to-day incubation patterns for individual females. He concludes that the majority of studies fail to demonstrate an increase in attentiveness as day of hatching approaches, that once "normal" attentiveness is reached it is maintained with irregular daily fluctuations to hatching. Kendeigh (1952:27, 169), however, suggests that there is an increase of attentive time, and a corresponding decrease of inattentive time, during the first three days, after which there is a rather constant fluctuation around a median giving in general a rather uniform attentive behavior.

My data are not sufficient to add materially to this question, although the pattern seems rather clear even if not definite. There appears to be an increase of attentiveness the first three days, with a slight falling off for the next three days, followed by an increase up to the eleventh day, and then a decrease during the last two days of incubation. Kendeigh (1952:169), discussing attentive behavior of many species, states that there is no evidence that the incubating birds consistently spend more time on the eggs during the latter days just before hatching. Certainly this appears to be the case for the Scarlet Tanager. Perhaps additional observations will smooth out the apparent irregularities of my data, especially, during the last two days. I would have expected a slight increase the first three days and then, as Kendeigh suggests, a slight variation around the median up to time of hatching.

Rain.—In general, the female Scarlet Tanager remains on her nest during rain. This does, of course, lengthen her sessions, but does not account for the longest observed sessions which actually occurred in clear weather. Sessions shorter than might be expected during rainy days may be accounted for in part by the fact that the female slips off the nest between showers. Moreover, because most nests are well sheltered by a leaf canopy overhead, she may leave the nest during a rain when the drops are not actually striking her on the nest.

Sunlight.—Although the Scarlet Tanager nest is well shaded, there are times when direct sunlight shines on the nest. I have never observed a female tanager to leave her nest when direct sunlight strikes her even though, at times, she appears uncomfortable, even opening her bill as if "panting." Even though constancy tends to decrease as temperature increases, this factor of sunlight on the nest may account, in part, for unexpected fluctuations at higher temperatures.

Temperature.—In general, there is an inverse relation between temperature and session length. The relationship demonstrated by my data is not as definite as one might wish it to be, yet it is quite evident from a consideration of the

TABLE 3

TEMPERATURE AND CONSTANCY DATA FOR THREE INCUBATING SCARLET TANAGERS

Female	Day of incubation	Per cent of constancy	Temperature F
10	3	90	61.6
"	2	89	66.2
"	7	87	68.3
"	5	85	67.7
"	4	84	67.0
"	1	82	76.2
"	6	58	79.6
17	9	92	56.0
"	11	88	64.9
"	10	87	61.5
"	8	87	74.5
"	12	85	71.5
"	13	71	80.3
18	4	76	67.0
"	3	70	64.8
"	1	65	78.3
"	5	47	76.7

patterns for the three females in Table 3. Day of incubation is included to show that as a factor, it is not as closely correlated as are temperature and constancy. For those temperatures 67 F and below, there is a definite increase in constancy as the temperature lowers, and considering those temperatures 75 F and over, there appears a corresponding decrease of constancy as temperatures increase. Kendeigh (1952:42), Skutch (op. cit.), and others have shown this correlation with a number of passerine bird species. The temperature effect, however, does not act in an isolated manner and must be considered as only one ingredient of the many affecting the female tanager's constancy.

Time of day.—Skutch (op. cit.) distinguished between the influence of temperature on incubation not only from the standpoint of colder or warmer days but by hourly variations within the day pointing out "that many birds spend more time on their eggs in the cool of the morning and evening than in the middle of the day when the air is usually warmer" etc. Kendeigh (1952: 170) likewise noted a decrease of incubating attentiveness in early or mid-afternoon and increase in the evening. My observations of the female Scarlet Tanager do not agree with this trend. The average of eleven "morning" (see paragraph 2) constancies is 74.8% and for ten "evening" is 71.1%, while the

average of sixteen "midday" is 78.8%, an apparent reversal of what has been found for similar passerine birds.

While the differences in the average constancies are not great and the sample is small. I believe the explanation is in part due to the feeding behavior of the female. In the morning after a long period without food, she tends to spend more time foraging, preening, and "exercising" after the night of immobility. Then she settles down to a more stable incubation pattern throughout the major portion of the day. In the late afternoon and just before dusk she becomes more active, searching for food and feeding while insects are plentiful and just prior to the approach of the long nonfeeding portion of the daily cycle.

Is high constancy of advantage?—Skutch (op. cit.) interestingly discusses this for several species from various standpoints, stressing that increased constancy might reduce the incubation period as well as lessen the hazards of egg loss to predators. There is no evidence, and I would expect none, that the increased constancy shortens the Scarlet Tanager incubation period. However, it seems to me that the more constant the incubating and inconspicuous female Scarlet Tanager is on the nest, the less opportunity for predator detection *unless* the increased constancy is the result of periodic feeding by her conspicuous mate, for I have found that it is the tanager activity itself which gives the nest location cue to predators.

SUMMARY

Incubation data on female Scarlet Tanagers, gathered in southern Michigan in 1947, 1948, and 1949 were reworked according to the formula presented by Skutch to determine Constancy of Incubation, giving an average constancy of 77% which lies within the range of Skutch's constancies. It is suggested that additional data be gathered for individual females wherever possible including day of incubation, time of day, and temperature and that these be analyzed in relation to the species constancies.

Various factors influencing the female Scarlet Tanager's constancy on the nest were discussed. Among those influencing constancy were: male feeding female on nest; male feeding female soon after she left the nest; temperature; time of day; sunlight; rain; and day of incubation. The interplay of all these factors influenced the individual female incubation patterns.

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